Anatomical relationships of the pia mater to cerebral blood vessels in man

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Using scanning and transmission electron microscopy and light microscopy, the authors studied the human pia mater and its relationship to the entry of blood vessels into the normal cerebral cortex. The purpose of this investigation was to examine the long-established concept that the subarachnoid space communicates directly with the perivascular spaces of the cerebral cortex. Brains obtained post mortem from subjects with recent subarachnoid hemorrhage (SAH) and purulent leptomeningitis were studied by light microscopy to determine the permeability of the pia mater to red blood cells and inflammatory cells. Scanning electron microscopy showed that the normal pia mater is a flat sheet of cells that is reflected from the surface of the brain to form the outer coating of the meningeal vessels in the subarachnoid space. Transmission electron microscopy confirmed that the cells of the pia mater are joined by junctional complexes and form a continuous sheet that separates the subarachnoid space on one side from the subpial and perivascular spaces on the other. Thus, neither the pia mater nor the subarachnoid space extends into the brain beside blood vessels as they enter the cerebral cortex. The perivascular spaces were, in fact, found to be confluent with the subpial space and not with the subarachnoid space. In cases of recent SAH, red blood cells did not enter the perivascular spaces from the subarachnoid space; neither did India ink injected post mortem into the subarachnoid space pass into the perivascular spaces. The results of these crude tracer studies suggest that the pia mater is an effective barrier to the passage of particulate matter. Histological examination of brains of patients who had died with purulent leptomeningitis showed that inflammatory cells were present in the cortical perivascular spaces and in the contiguous subpial spaces. The presence of a large number of inflammatory cells in the subarachnoid space suggests that inflammatory cells readily penetrate the pia mater that separates the perivascular spaces from the subarachnoid space. The permeability of the pia mater to small molecular weight substances is briefly discussed.

**Key Words** • pia mater • cerebral blood vessel • ultrastructural study • anatomical study

For many years it has been generally accepted that there is a direct anatomical communication between the subarachnoid space and the perivascular spaces at the surface of the brain and spinal cord. Evidence to support this assumption has been derived from light microscopy studies over the last century and, more recently, from electron microscopy and tracer studies. In their review in 1954, Woollam and Millen expounded the accepted view that vessels enter the brain from the subarachnoid space and carry with them extensions of the arachnoid coating of the vessel and a layer of pia mater. This extension of the leptomeninges was described as the reticular perivascular sheath and broadly corresponded to the "Piagliamembran" of Schaltenbrand and Bailey. It was proposed that the perivascular space lay between the layers of the reticular perivascular sheath. This perivascular space carries the eponymous term "Virchow-Robin space" and was thought to be continuous with the subarachnoid space.

The long-standing interest in the anatomical arrangements of vessels as they enter the brain led to the description of several spaces, such as the "perineuronal spaces" of Obersteiner and the "epispinal" and "perivascular spaces" of His. Woollam and Millen came to the conclusion that the perineuronal spaces were artifactual, as were the perivascular spaces of His. They found the epispinal space of His difficult to interpret as they considered that the original descriptions were unclear. Many of the arguments regarding the structure of perivascular sheaths and the disposition of perivascular spaces have been resolved by the introduction of...
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electron microscopy. The eponymous term "Virchow-Robin space" remains to describe the space between blood vessel and nervous tissue as vessels enter or leave the surface of the brain or spinal cord.

In this study we reexamine the structure of the human pia mater, the relationship of the pia to the entry of blood vessels in the cerebral cortex, and the concept that the subarachnoid space is in continuity with the perivascular spaces of the brain. From our initial scanning electron microscopy (SEM) observations, it became clear that the pia mater was a sheet of cells that was reflected onto vessels in the subarachnoid space rather than following vessels into the cerebral cortex. This anatomical arrangement appeared to preclude a direct communication between the subarachnoid space and the perivascular spaces as suggested by previous authors. As suitable in vivo tracer studies in human brains were not feasible, a crude system of India ink injection into the subarachnoid space at postmortem examination was employed to test the permeability of the pia mater to particulate matter. In addition, specimens of brain from subjects with recent subarachnoid hemorrhage (SAH) and from others with purulent leptomeningitis were examined in order to determine the permeability of the pia mater to red blood cells and inflammatory cells. The results of these studies strongly suggested that the perivascular spaces are in continuity with the subpial space but that both these spaces are separated from the subarachnoid space by an intact layer of pia mater.

Materials and Methods

Blocks of parietal and frontal lobe cortex and overlying leptomeninges were taken post mortem from 10 normal subjects (age range 42 to 91 years) and from three formalin-fixed biopsy specimens of normal frontal lobe removed during surgical excision of cerebral tumors. Similar specimens of brain were obtained post mortem from four subjects with recent SAH (age range 40 to 56 years), all of whom died 1 hour to 8 days following the rupture of a saccular aneurysm, and from three subjects with purulent leptomeningitis (age range 7 to 83 years). Seven of the normal brains were acquired from recent SAH, and brain from cases of leptomeningitis were stained with hematoxylin and eosin (H & E), hematoxylin van Gieson, and the Gordon and Sweet method for reticulin. Red blood cells in cases of SAH were visualized by treatment of deparaffinized sections with diaminobenzidine and hydrogen peroxide; the presence of peroxidase on the red cell membranes results in a brown reaction product.

India Ink Preparations

To test the permeability of the pia mater to particulate matter, 5 ml of undiluted Rotring India ink, in which over 90% of the particles were less than 1 μm in diameter, was injected manually through a fine-gauge needle into the subarachnoid space of the frontoparietal region of three normal brains at autopsy. The black-stained areas of meninges and underlying cortex, measuring 5 to 6 cm in diameter, were excised and cut into blocks 1-cm thick. Following fixation in formalin, the

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* Critical-point dryer and sputter coater manufactured by Polaron Instruments, Inc., Hatfield, Pennsylvania.
† Scanning electron microscope manufactured by Japan Electron Optics Laboratory, Nakagami-cho, Akishima City, Tokyo, Japan.
‡ Transmission electron microscope manufactured by Philips Electronic Instruments, Mount Vernon, New York.

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tissue was embedded in paraffin wax and serial 5-µm thick sections were stained with H & E for light microscopy.

Results

Normal Brain

Scanning Electron Microscopy. Most of the information derived from SEM in this study was obtained from examining the subarachnoid space of normal brains. Specimens that had received subarachnoid injections of glutaraldehyde to expand the subarachnoid space proved to be the most suitable for SEM. In cases of SAH and meningitis, the presence of blood and pus did not allow a clear view of the subarachnoid vessels or pia on SEM. A lower-power scanning electron micrograph of a normal cerebral sulcus cut transversely is seen in Fig. 1. The sulcus runs vertically down the photograph, and the outer layer of the arachnoid passes horizontally across the top of the picture. A vessel is suspended in the subarachnoid space by thin arachnoid chordae as described by Arutiunov. The pia mater and basement membrane of the glia limitans have been focally separated from the underlying brain in the lower part of the sulcus to reveal the glia on the surface of the cortex.

When a sulcus is bisected longitudinally, its lateral walls are exposed to reveal the subarachnoid vessels and the pial surface (Fig. 2). Histological examination showed the vessel in Fig. 2 to be an artery; it spread its branches over the pia mater, and the smaller branches ultimately disappeared from view toward the underlying cortex. As the branches of the artery passed from the subarachnoid compartment, the outer coatings of these vessels expanded as fan-like structures (Figs. 2 and 3) that were continuous with the pia mater on the surface of the brain. Thus, the subarachnoid space does not seem to connect with the perivascular spaces of the cortex. Small perforations were seen in the pia (Fig. 3), but it was difficult to determine whether these were real gaps or artifactual tears in the pia. One vessel branch in Fig. 2 did appear to enter a hole in the pia, but this may well be an invagination of the pia rather than a perforation. Fine chordae passing between the pia and the vessels in the subarachnoid compartment were also clearly demonstrated (Figs. 2 and 3). In most specimens examined, the vessels passed obliquely from the subarachnoid compartment and ran for some distance under the pia mater before entering the brain. These vessels in the subpial space could be detected because they raised a ridge under the pia mater.

Transmission Electron Microscopy. In sections of normal cerebral cortex and overlying leptomeninges, the outer arachnoid mater was identified as a structure formed from three or four layers of attenuated cells and intervening bundles of collagen fibers. The outer arachnoid was distinct and clearly separated from the underlying thin layer of pia mater. The relationship of the pia mater to a small blood vessel as it enters the cerebral cortex is shown in Fig. 4 upper left. The pia was shown as a continuous layer of cells broken only by artifactual tears. It separated the subarachnoid space from the subpial space in which there were isolated cells and bundles of fine collagen fibers. No continuous layer of pial cells accompanying the vessel into the cortex was seen. Thus, it appeared that the perivascular space was continuous with the subpial space rather than with the subarachnoid space. Small collagen fibers in the perivascular space separated the ruffled surface of the cortical glia limitans with its investing basement membrane (Fig. 4 upper right) from the cells of the vessel wall. The pia mater itself (Fig. 4 lower) consisted of one to three layers of attenuated cells forming intercellular junctions, most of which had the morphology of gap junctions and desmosomes. An incomplete amorphous structure resembling basement membrane partly coated some cell layers (Fig. 4 lower).

Light Microscopy. The preceding scanning and transmission electron microscope studies suggested that the pia mater forms a cellular layer interposed between the subarachnoid space and the perivascular spaces of the cortex. The object, therefore, of the India ink injections and the examination of brains following SAH was
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FIG. 2. Scanning electron micrograph of the lateral wall of a normal cerebral sulcus. An artery in the subarachnoid space is seen spreading its branches over the sheet-like pia mater (pia). As branches of the artery disappear from view, the outer leptomeningeal coat of the vessel fuses with the pia mater as a fan-like structure (black arrow). A vessel branch in the center of the picture appears to pass into a deep hole (open arrow), which is probably an invagination of the pia. Thin chordae run between the pia and vessels. × 100.

to see whether particulate matter does or does not enter the cerebral perivascular spaces from the subarachnoid space.

Sections of leptomeninges and cerebral cortex showed that India ink was distributed throughout the subarachnoid space adhering to arachnoid chordae and trabeculae. India ink also coated the arachnoid surface of the subarachnoid vessels but did not penetrate the vessel walls themselves. Examination of the zones where vessels entered the cerebral cortex (Fig. 5) showed that India ink filled funnel-like invaginations of the subarachnoid space but did not penetrate the perivascular spaces of the cortex.

Subarachnoid Hemorrhage

Red blood cells filled and distended the subarachnoid space in the histological sections from three patients with SAH who died 1 hour to 8 days after rupture of a saccular aneurysm. However, despite the distention of the subarachnoid space by erythrocytes, red blood cells did not pass into the cortical perivascular spaces (Fig. 6).
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Leptomeningitis

When sections of leptomeninges and cerebral cortex were stained with the Gordon and Sweet reticulin technique in cases of meningitis, several black-stained layers were identified (Figs. 7 and 8). These included the reticulin in the walls of the subarachnoid and intracerebral vessels; reticulin associated with the arachnoid coating of subarachnoid vessels; reticulin (small collagen fibers) in the pia mater and subpial space; and the basement membrane of the glia limitans. The perivascular spaces of subarachnoid vessels were expanded by inflammatory cells that accumulated between the arachnoid coat and the vessel wall (Fig. 7 left). On the surface of the brain, a ragged fibrillary layer, representing the collagen fibers of the pia, was separated by inflammatory cells from the smooth linear basement membrane of the glia limitans (Fig. 7 left). As branches of meningeal vessels entered the brain, the pia was seen to fuse with the outer coating of the vessel (Fig. 7 center). Thus, the perivascular spaces surrounding vessels as they entered or left the cortex were bounded on their outer aspects by the basement membrane of the glia limitans and on their inner aspect by the adventitia of the vessel wall (Fig. 7 right). The continuity of the subpial space with the perivascular spaces could be clearly seen (Figs. 7 right and 8); both spaces were expanded by inflammatory cells and were separated from the subarachnoid space by pia mater and its associated reticulin or collagen fibers. Occasional gaps in the reticulin layer of the pia were seen (Fig. 7 right) and probably allowed the passage of inflammatory cells from the perivascular and subpial spaces into the subarachnoid space. As noted in the preparations examined by SEM, vessels often tended to lie obliquely on the surface of the cortex in the subpial space. Figure 8 shows a vessel entering the brain obliquely with a layer of pia and associated connective tissue separating it from the subarachnoid compartment; the pia mater does not enter the brain substance with the vessel.

Fig. 4. Upper Left: Transmission electron micrograph (TEM) showing the entry zone of a small blood vessel at the surface of normal cerebral cortex. A continuous layer of pia mater (p) separates the subarachnoid space (SAS) from the subpial space (SPS). As the vessel enters the cortex, the subpial space extends along the outside of the vessel as the perivascular space (long arrows), × 2200. Upper Right: Higher-power TEM of the region marked by the lower of the two long arrows in upper left. The irregular surface of the cortical glia limitans can be seen at the bottom of the figure, and its basement membrane is separated from the vessel wall by the subpial-perivascular spaces (SPS-PVS) containing sparse collagen fibers, × 10,700. Lower: Higher-power TEM of the pia mater. Thin cell processes partly coated by a structure similar to basement membrane (b) separate the subarachnoid space (SAS) from the subpial space (SPS). The intercellular junctions (j) are also shown, × 33,150.
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Although reticulin stains revealed the separation of the pial connective tissue and the basement membrane of the glia limitans in cases of leptomeningitis, the cellular layer of the pia could not be directly demonstrated in these preparations. However, the relationship of the pia to the entry of blood vessels into the brain in Fig. 8 is similar to that shown in Fig. 4 upper left, which suggests that reticulin staining does accurately reflect the positions of both the pia and the basement membrane of the glia limitans.

Discussion

Scanning electron microscopy of the cerebral leptomeninges of normal human brain in the present study has shown that the pia mater forms a sheet that is reflected from the surface of the brain onto the vessels of the subarachnoid space. The pia is continuous with the meningeal coating of the vessels. By this anatomical arrangement, the pia mater separates the subarachnoid space on the one side from the subpial and cortical perivascular spaces on the other. Transmission electron microscopy confirmed the sheet-like nature of the pia, which is composed of thin layers of cells that form junctional complexes at their margins. The only gaps appear to be artifactual. Although dissociated elongated cells were present in the subpial space, no continuous layer of pia was seen accompanying vessels into the brain. A diagrammatic representation of the relationships between the leptomeninges, vessels, and cerebral cortex in man has been constructed from the data in this study and is illustrated in Fig. 9.

If the pia mater forms a barrier between the subarachnoid and underlying subpial and perivascular spaces, it would be of great value to know the permeability characteristics of this barrier. It is not possible to perform in vivo tracer experiments in man, so an attempt was made in our present study to gain information from crude postmortem India ink injections and from the study of "natural" tracers such as blood and pus. The results of the India ink injections suggested that the pia obtained post mortem was not permeable to particulate India ink. Similarly, examination of brains following recent SAH showed that red blood cells did not flow into the subpial or perivascular spaces but were confined to the subarachnoid space (Fig. 9B). Blood is often widely distributed through the subarachnoid space in patients dying soon after SAH, red blood cells even permeate the network of channels in arachnoid granulations. If a free connection exists between the subarachnoid space and perivascular spaces, red blood cells

![Fig. 5. Photomicrograph following India ink injection into the cerebrospinal fluid of normal brain. There is a funnel-like invagination of the subarachnoid space (SAS) by the ink but no penetration of the perivascular space as the vessel enters the cortex. The brain is artifactually retracted from the vessel. H & E, × 300.](image)

![Fig. 6. Photomicrograph of a specimen from a subject who died after subarachnoid hemorrhage. Red blood cells (seen black) fill the subarachnoid space at the top of the figure and the lumen of the cortical vessel in the center but have not entered the barely visible perivascular space (ps). The artifactual space (as) between the vessel and the brain is not the true perivascular space. Diaminobenzidine and hematoxylin, × 300.](image)
FIG. 7. Photomicrographs of a specimen from a subject who died of leptomeningitis. Gordon and Sweet reticulin stain. 

Left: Inflammatory cells fill the subarachnoid space (SAS) and separate the arachnoid coating (A) from subarachnoid vessels. Connective tissue of the pia mater (p) is separated from the basement membrane of the glia limitans (b) by the subpial space. A vessel enters the cortex in the lower left portion of the figure. × 300.

Center: A branch from a large subarachnoid vessel at the top of the figure enters the cortex. The pia mater (p) fuses with the outer coating of the vessel. Subpial inflammatory cells separate the pia mater from the basement membrane of the glia limitans (b). × 300.

Right: As the vessel in the center of the figure enters the cortex, it is surrounded by a perivascular space (ps) that is expanded by inflammatory cells and is in continuity with the subpial space between the pia mater (p) and the basement membrane of the glia limitans (b). There are focal gaps in the pia mater. SAS = subarachnoid space. × 470.

should track along the perivascular spaces. The failure of erythrocytes to enter the perivascular spaces in patients with SAH suggests that the pia mater does form an effective barrier to particulate matter.

A very different picture from that seen in SAH cases was observed in cases of leptomeningitis with regard to the permeability of the pia mater. In leptomeningitis, polymorphonuclear leukocytes and macrophages were distributed throughout the subarachnoid space and the subpial and perivascular spaces. Inflammatory cells even expanded the perivascular compartments of the meningeal arteries separating the arachnoid coating of the vessel from the vessel wall; this perivascular compartment is probably confluent with the subpial space and the cerebral perivascular space as suggested in Fig. 9C. The wide distribution of the inflammatory cells indicates that they are able to migrate from the blood vessel lumina, through the vascular endothelium, into the perivascular spaces and to penetrate the pia on the surface of the brain or to traverse the arachnoid coating of the subarachnoid vessels. There are many illustrations in the literature of polymorphonuclear leukocytes and macrophages passing between cells that are normally joined by intercellular junctions. It does not seem essential, therefore, to postulate the presence of permanent pores in the pia mater to allow the passage of inflammatory cells from perivascular spaces to the subarachnoid space since these cells could well penetrate the pia mater by the dehiscence of intercellular junctions.

Although the observations in the present study strongly suggest the anatomical arrangements for the pia mater as illustrated in Fig. 9, previous authors have drawn different conclusions from their studies. A review of the relevant literature, however, reveals several major reasons for this discrepancy and points to possible areas of misinterpretation. Early light microscopy studies of the meninges and the mode of entry of vessels into the cerebral cortex were limited by the techniques available and were more often concerned with distinguishing real perivascular spaces from the artifactual perineuronal spaces in this region. The reticulin stain employed by these authors to examine the meninges and vessels was similar to that used in the present study. However, with this technique alone it is difficult to distinguish between the pia and the glia limitans in normal brain.
Under normal circumstances, the pia mater is closely attached to the basement membrane of the glia limitans on the surface of the cerebral cortex. Similarly, the perivascular glial basement membrane is closely adherent to the walls of vessels within the normal brain so that the perivascular compartment containing collagen fibers and flattened cells is not usually detectable by light microscopy. In inflammatory disorders of the brain, however, inflammatory cells accumulate in the perivascular spaces and separate the basement membrane of the glia limitans from connective tissue of the blood vessel adventitia. Therefore, by examining brain tissue from cases of purulent meningitis, it was possible to define the perivascular spaces in the brain and to determine their relationship with the subpial and subarachnoid spaces. Although Millen and Woollam demonstrated the expansion of the perivascular spaces in inflamed brain, they did not describe the relationship of the pia mater to vessel entry zones in cases of meningitis and thus failed to appreciate the relationship between the subarachnoid, subpial, and perivascular spaces.

It was not until electron microscopy was used that different layers of the pia and glia limitans were defined. In some animals such as the mouse, the arachnoid and pia are very thin with little subarachnoid space between the outer arachnoid layer and the loosely associated cells and connective tissue of the inner pial layer. More defined structures are seen in the rat in which the pia forms a layer separated from the basement membrane of the glia limitans by collagen fibers. Of the various species studied, however, none seems to have a pia mater that is as substantial as that seen in man. Some authors have shown elongated cells in the perivascular spaces of vessels as they enter the cortex and assumed that they were meningeal in origin. They also suggested that the subarachnoid space accompanied the vessels into the brain as the perivascular space. Nevertheless, identification of meningeal cells in the perivascular compartments was rather tenuous. There are no definite markers for these cells, and usually the flattened cells described are dissociated from one another within the adventitia of the cortical vessels and do not form a continuous sheet. Some accounts of animal leptomeninges have, in fact, shown similarities to the arrangement seen in man in the present study, with pial cells reflected from the cortex onto subarachnoid vessels. In Fig. 1 of his light and electron microscopy studies in the cat, Jones showed pia mater and subpial vessels in a very similar arrangement to that seen in Fig. 3 of our present study. However, he assumed that the vessels had pierced the pia mater.
before entering the brain and that an extension of the subarachnoid space had accompanied the vessel as the perivascular space.

There have been few electron microscopy studies of the pia mater in man. Ramsey19 examined surgically removed human cerebral cortex, but her investigations concentrated mainly upon the demonstration of the irregular nature of subpial astrocytes forming the glia limitans. Although she stated that the pia mater did not always form a continuous layer over the surface of the brain, she offered no clear picture of human pia, and her main illustration of dissociated meningeal cells associated with the surface of the glia limitans was taken from the rat.

Previous SEM studies of pia mater and vessels entering the central nervous system in dogs,5 cats, and rabbits12 have suggested that the anatomical arrangement in these animals is similar to that shown in man in the present study. Cloyd and Low5 demonstrated that subarachnoid vessels blended with the pia on the surface of the dog spinal cord in a manner similar to that seen in the human cerebral cortex. Krahn12 examined the vessel entry zones in various parts of the cat and rabbit brain, and described how the leptomeningeal coat of the subarachnoid vessel was reflected onto the pia mater. Penetration of the pia mater and arachnoid coating of subarachnoid vessels by macrophages has also been observed in normal pia mater. Breaks in the connective tissue layers of the human pia mater were observed in leptomeningitis in the present study; such perforations could represent points of penetration of inflammatory cells or they may be artificial breaks in the delicate pia. Fenestrations in the leptomeningeal coating of the normal dog spinal cord have been described,2 but preliminary studies of human spinal meninges in our laboratory (DS Nicholas and RO Weller, unpublished data, 1986) suggest that the large holes are in an intermediate layer of arachnoid and that the pia mater on the surface of the cord is imperforate.

Although the results of our present study suggest that the pia mater forms a barrier to red blood cells and other particulate matter, its role as a barrier to nonparticulate matter remains to be fully elucidated. In the experiments performed by Weed25 over 60 years ago, potassium ferrocyanide:iron ammonium citrate solutions and India ink were perfused into the subarachnoid spaces of dogs and cats. In normal animals, neither tracer entered the perivascular spaces of the brain. Upon intravenous injection of strongly hypertonic solutions, however, both the ferrocyanide:citrate solution and India ink entered the perivascular spaces of the brain. Because Weed25 assumed that the subarachnoid and perivascular spaces were confluent, he concluded that the penetration of tracers into the perivascular spaces following the injection of hypertonic solution was due to alterations in fluid flow along the perivascular spaces. Another possible explanation is that the injection of hypertonic solutions altered the permeability of the intercellular junctions of the pia mater, thus allowing diffusion of the solution and of India ink through the previously impermeable pia and into the subpial and perivascular spaces. The results of more recent studies have also suggested that the exchange of many lipid-soluble and small molecular weight substances between the subarachnoid cerebrospinal fluid (CSF) and the brain is not very effective,1 although it was proposed that the lack of penetration was due to rapid clearance in the CSF.

Conflicting somewhat with the results of Weed25 are the findings of Rennels, et al.20 who showed that horseradish peroxidase, injected into the subarachnoid space of cats and dogs, is widely distributed through the perivascular spaces within 6 minutes. These findings suggest that the pia mater in the cat and dog is highly permeable to horseradish peroxidase. If a differential permeability of the pia mater does exist whereby different substances cross the barrier at different rates, it may have important implications for the therapeutic use of intrathecal injections. It may also be necessary to take the permeability of the pia into account when predicting the effects upon intracerebral vessels of agents released during SAH. Arterial spasm following SAH and its consequences have been well recorded,46 and the pathological changes of intramural hemorrhage and subintimal thickening have been correlated with spasm of larger subarachnoid vessels following SAH.22 Separation of the subarachnoid space from the subpial and cortical perivascular spaces by the pia mater may offer some protection to vessels in the brain from vasoconstrictive agents in the CSF.

Conclusions

As a general conclusion to this study, it appears that the pia mater is composed of a sheet of cells, joined by intercellular junctions, that separates the subarachnoid space from the subpial and perivascular spaces of the brain. This pial barrier appears to be impermeable to particulate matter, such as red blood cells, but permeable to migrating inflammatory cells. However, its permeability characteristics to small and large molecular weight solutes remain to be elucidated and could depend upon the capacity of these substances to pass through the intercellular junctions which join the cells of the pia mater.

Acknowledgments

The authors would like to thank the staff of the Electron Microscope Unit and Neuropathology Laboratory, Southampton General Hospital, for technical assistance and advice; Peter Jack for the drawing in Fig. 9; and Margaret Harris for secretarial assistance.

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Manuscript received October 15, 1985. Accepted in final form February 19, 1986. This study was supported by the Wessex Neurological Centre Brain Tumour Research Fund.

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